

Is quantity or quality of food influencing the reproduction of rice-field rats in the Philippines?

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Abstract

Context. Asynchronous or aseasonal planting of rice crops can extend the period when high-quality food is available to rodents. Consequently, rodents may extend their breeding season, increasing population densities. An improved understanding of the effects of food availability and quality on rodent reproduction may enable better forecasts of high rodent population densities in response to asynchronous or aseasonal planting of crops.

Aim. The present study examined the association between the quality and quantity of food and the reproductive success of female rice-field rats, *Rattus tanezumi* and *Rattus argentiventer*, in a lowland rice landscape in the Philippines.

Methods. We evaluated the main dietary components of female rats on two different islands through a cropping season during the 2010 wet season. The breeding performance of 60 female *R. tanezumi* and 60 *R. argentiventer* individuals was measured.

Key results. Our findings indicated the following: (1) the main dietary items for females of both rodent species during the main breeding season (the booting stage to harvest) were rice panicles and rice seeds; (2) the high protein content of the rice crop at the tillering stage triggered the onset of the main breeding season, leading to the highest rates of conception during the booting and ripening stages; (3) the quantity of food available at the stubble stage provided sufficient nutrient to maintain pregnancy and lactation by females; and (4) asynchronous planting and poor harvest technology could extend the breeding season of rice-field rats.

Conclusions. We contend that the extension of the growing season by 3–4 weeks provides high-quality food for rodents, which in turn provides sufficient conditions for higher population densities. The availability of spilled rice grain at the stubble stage is a source of good-quality food for pregnant and lactating females, allowing extension of the breeding season.

Implications. Synchronous planting (within 2 weeks) with good post-harvest management of rice stubble are important to prevent high population densities of rice-field rats in lowland rice landscapes in the Philippines.

Additional keywords: breeding ecology, diet composition, food quality, food quantity, irrigated rice, *R. tanezumi*, *R. argentiventer*, synchronous cropping.

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Introduction

In Asia, pre-harvest losses caused by rodents can be equivalent to the amount of food that could feed 450 million people for 12 months (Singleton *et al.* 2008). Rodent damage is more serious in South-east Asia where cropping frequency has increased from one to two or three rice crops per year such as occurs in regions of Indonesia and Vietnam. Rodent losses are higher when crops are planted aseasonally and asynchronously in response to El Niño or La Niña events (e.g. Indonesia; Sudarmaji *et al.* 2010), typhoons (e.g. Myanmar; Htwe *et al.* 2013) or changing agricultural practices (e.g. Myanmar, Vietnam; Singleton *et al.* 2007, 2010). Asynchronous or aseasonal planting of rice can provide high-quality food for

rodents for longer periods of time per year and extend their breeding season. An increase in breeding performance is often the main reason populations reach high densities (Lam 1983; Huan *et al.* 2010; Sudarmaji *et al.* 2010; Htwe *et al.* 2012).

The quality of food can influence the reproductive ability of rodents (Negus and Pinter 1966; Reichman and Van De Graaff 1975; Bomford 1987a) and could be an important driver of high population densities in agricultural landscapes (Leirs *et al.* 1994; Ylönen *et al.* 2003). In South-east Asia, our understanding of the role of food quantity and quality on the population dynamics of rodents is less well understood, with only one study on *Rattus argentiventer* in An Giang province in the Mekong

delta of Vietnam (My Phung *et al.* 2011). An increase in our understanding of the factors that influence the breeding dynamics of rice-field rats could lead to better forecasts of high rodent populations. In turn, this would provide smallholder farmers in the Philippines the ability to take proactive actions for rodent management before high populations of rodents develop. We hypothesised that the quality of food is more important than quantity of food for influencing reproductive success of female *R. tanezumi* and *R. argentiventer*. To identify the impact of quality and quantity of food on reproduction, (1) the proportion of breeding females (pregnant and lactating) and litter size were analysed to identify the effect of the stage of the rice crop on breeding performance, (2) the main dietary components of female rats at four main crop stages of rice plant were assessed, (3) the protein content of the rice plant (quality) at different crop stages was analysed, and (4) the amount of available food (quantity) 2 weeks after harvest was measured.

Materials and methods

Study sites

Laguna

Masiit Barangay (smallest political division, 14°1'23"N, 121°6'10"E in Calauan, Laguna; hereafter referred to as Laguna) is located at 21 m above sea level. The soils are predominantly eutric gleysol (as defined by FAO) or tropaquept (as defined by USDA). The mean annual rainfall (1979–1992) is 2090.7 mm (maximum 323.7 mm in July and minimum 17.8 mm in February). The dry season is from December to April and the wet season from May to November. Mean annual temperature is 27.3°C, reaching its highest mean monthly maximum in April and May (34.1°C) and lowest mean monthly minimum in December (26.1°C). Mean relative humidity is 88%, with the lowest in May (71%) and the highest in September–October (90%). Most farmers practice lowland irrigated rice-monoculture cropping and grow two rice crops per year. The first crop is planted in January and the second crop in June or July, depending on the schedule of irrigated water. Permanent channels run along the perimeter of the farming areas, with smaller channels traversing the fields, supplying water for irrigation. The main rodent species in the rice field is *Rattus tanezumi*.

San Jose

The study was conducted in Central Barangay (12°44'N, 121°35'E) in San Jose, Mindoro, the Philippines. The rice crops are lowland-irrigated, with two rice crops a year, namely, a wet-season crop (from May–November) and a dry-season crop (from November–April) (see more details in Htwe *et al.* 2012). The main rodent species in the rice fields are *R. argentiventer* and *R. tanezumi*.

Stomach-content analysis

During the wet season of 2010, the stomachs of female rats were collected at each major crop stage of rice (tillering, booting, ripening and stubble stages). Stomachs were preserved in 70% ethanol and kept at <10°C until examined. The contents of each stomach were washed under running water on a sieve (0.16 mm),

subsampled and poured evenly over a microscopic glass slide. A sample was mounted on a slide with polyvinylpyrrolidone (PVP) (Tann *et al.* 1991). PVP was used as a reagent to make samples clearer and to coat the samples so that they could be observed again if needed. If any plant fragment could not be identified, leptophenol solution was used to provide a clearer view of the structure of the plant tissue (My Phung *et al.* 2011). Each of the observed dietary particles was classified into the following categories by using reference pictures from My Phung *et al.* (2011): monocotyledonous plant materials (leaves, roots), monocotyledonous grains, dicotyledonous plant materials, coconut meat, insects, snails and/or crabs, digested monocotyledonous plant parts, digested animal tissues and unknown material (unidentified debris). The size of each particle was estimated by eye and the scores were totalled per category and transformed to percentages.

Collection of rodents

Female adult rats caught in Laguna and San Jose during the 2009 and 2010 wet season were collected to determine their breeding performance at the same four crop stages (see details in Htwe *et al.* 2012).

Background food availability

Food supply in and around the rice fields was sampled 2 weeks after harvest. Twenty 1-m² samples were selected inside the rice field and on the levee of the rice fields, by using systematic random sampling. The sampling was modified from a previous study developed for wheat fields in Australia (Ylönen *et al.* 2003). If the soil was still moist and grains were immersed in the soil, then soil was removed to a depth of 50 mm and samples were placed into a cloth bag, along with any aboveground vegetation. The samples were air-dried to 14% moisture and rice grains were separated from the soil and other vegetation, and then weighed.

Seed nitrogen and protein assays

At the seedling stage, tillering stage, maximum tillering stage and early flowering stage (booting stage) of the rice crop, 50 tillers were randomly sampled for nitrogen and protein assays. Tillers were hand-clipped at ground level and leaves were cleaned under running tap water. Samples were put in an oven and dried overnight at 80°C. To obtain homogeneous powder, samples were finely ground with a Cyclone Udy Mill (UDY Corporation, Fort Collins, CO, USA; www.udyone.com, verified 18 March 2014) with a stainless steel screen and a 20-mm-mesh sieve. Ground samples were transferred to tightly capped glass jars or sealed polyethylene bags, and stored for further analysis. At ripening stage, 50 heads of rice grain were randomly sampled 2 weeks before harvest. Seeds were separated from heads and hulls, stems removed, and dried to 14% moisture. A sample of 30–50 g of the clean seeds was pounded into a fine powder for assay. Two subsamples of clean seeds (30–50 g) were collected 2 weeks after harvest and were tested for nitrogen content; one from spilled grain inside the rice field and the other from the levee of the rice fields. Total nitrogen and protein contents in rice tillers and grains were determined by the semi-micro

Kjeldahl method and the conversion coefficient was 5.95 (FAO 2003).

Data analyses

The effect of region on the diet composition and breeding performance of *R. tanezumi* was tested using a generalised linear model. Note that *R. argentiventer* has not been previously reported in Laguna on Luzon Island. Our trapping confirmed this, so we did not analyse the effect of region for *R. argentiventer*. The dietary compositions of monocotyledonous plant materials and monocotyledonous grains at different crop stages were compared by the use of a generalised linear model with crop stage as a predictor. Multinomial regression analyses were conducted to determine the effect of crop stage and diet on the proportion of breeding females and litter size. We conducted also AIC analysis and the findings were the same (see Table S1, available as Supplementary Material for this paper). *Post hoc* comparison was conducted to compare the proportion of monocotyledonous plant materials and monocotyledonous grains, and litter size at different crop stages. Student's *t*-test was used to compare the protein content at different crop stages and the amount of background food between sites. All statistical analyses were carried out in SPSS version 13.0.

Results

Only *R. tanezumi* was captured in and around rice fields in Laguna. Both *R. tanezumi* and *R. argentiventer* were captured in Mindoro. There were significant differences in diet compositions ($F_{1,19}=6.85$, $P\leq 0.01$) and breeding performance ($F_{1,54}=2.35$, $P\leq 0.04$) of *R. tanezumi* between regions. Therefore, we analysed these parameters separately for each site.

Diet composition and breeding performance of *R. tanezumi* in Laguna

In Laguna, the diet components of 15 female rats were monocotyledonous plant parts, monocotyledonous grains, coconut meat, snail and crabs, insects, dicotyledonous plant parts, digested monocotyledonous grains and unidentified plant debris. The major components of the stomach contents at the tillering, booting and stubble stages were monocotyledonous plant parts (91%, 94% and 62%, respectively), whereas at the ripening stage, the major components were monocotyledonous grains (52%) and monocotyledonous plant parts (41%) (Fig. 1a). The mean (± 1 s.e.) composition of monocotyledonous plant parts in the diet at the booting ($95 \pm 2.8\%$, $P < 0.01$) and tillering stages ($92 \pm 3.5\%$, $P < 0.01$) were higher than at the stubble ($62 \pm 2.8\%$, $P < 0.11$) and ripening stages ($41 \pm 2.8\%$). No monocotyledonous grains were found in stomachs at the tillering and booting stages of the rice crop. The presence of monocotyledonous grains at the ripening stage ($52 \pm 2.4\%$) was significantly higher than that at the stubble stage ($23 \pm 7.5\%$; $F_{1,39}=7.70$, $P \leq 0.01$).

Female *R. tanezumi* bred throughout the crop season in Laguna. The proportion of lactating and pregnant females was different at different crop stages. No lactating females were captured at the booting stage. The proportion of pregnant females was higher than that of lactating females at the

ripening stage (29% pregnant) and stubble stage (38% pregnant). The proportion of lactating females was equal or greater than that of pregnant females at the stubble stage (Fig. 2a). There was a significant change in the proportion of breeding females (both pregnant and lactating) among the crop stages ($R^2=0.242$; $F_{3,278}=18.942$; $P < 0.001$), with the highest proportion occurring at the ripening stage and lowest at the tillering stage. The proportion of breeding females increased with the increase in monocotyledonous grains and monocotyledonous plant parts in the diet ($R^2=0.124$, $F_{1,46}=7.076$, $P=0.011$, and $R^2=0.129$, $F_{1,55}=8.162$, $P=0.006$, respectively).

The mean litter size of *R. tanezumi* in Laguna was 8.7 ± 1.06 ($n=33$). The effect of different crop stages on mean litter size was significant ($R^2=0.525$, $F_{1,48}=6.642$, $P=0.030$). The mean (± 1 s.e.) litter sizes at the ripening (9.1 ± 0.39) and booting (9.3 ± 0.45) stages were similar ($P=0.39$), but significantly higher than those at the tillering (8.0 ± 0.25 , $P < 0.01$) and stubble (7.2 ± 0.69 , $P < 0.01$) stages. The litter size increased with the increase of monocotyledonous grains in the diet ($R^2=0.135$, $F_{1,40}=6.235$, $P=0.017$).

Diet composition and breeding performance of *R. tanezumi* in San Jose, Mindoro

In San Jose, the diet components of female *R. tanezumi* over the monsoon rice season were monocotyledonous plant parts, monocotyledonous grains, snails (and crabs), coconut meat, dicotyledonous plant parts and insects. The major components in the diet of the female rats at specific stages of the rice crop were as follows: monocotyledonous plant parts at the tillering stage (41%); snail and crab (36%) and monocotyledonous plant parts (29%) at the booting stage; monocotyledonous grains (43%) and monocotyledonous plant parts (34%) at the ripening stage; and monocotyledonous grains at the stubble stage (43%) (Fig. 1b). There was no significant difference in the composition of monocotyledonous plant parts in the diet of *R. tanezumi* in San Jose among crop stages. The proportion of monocotyledonous grains at the stubble ($44 \pm 9.5\%$, $P < 0.01$) and ripening ($43 \pm 7.5\%$, $P < 0.01$) stages was higher than that at the tillering ($14 \pm 4.3\%$) and booting stages ($13 \pm 0.1\%$).

Female *R. tanezumi* bred throughout the crop season in San Jose. The proportion of pregnant females was higher than that of lactating females at ripening and stubble stages, whereas proportions of both were equal at the tillering stage. No lactating females were captured at the booting stage. Overall, the crop stage was not a good predictor of increasing proportion of breeding female *R. tanezumi*. The proportion of breeding females (both pregnant and lactating) increased with the increasing proportion of monocotyledonous grains in the diet ($R^2=0.124$, $F_{1,55}=7.08$, $P=0.011$). However, the component of monocotyledonous plant parts was not a good predictor for the proportion of breeding females (Fig. 2b).

The mean litter size of *R. tanezumi* in San Jose was 6.00 ± 2.34 ($n=22$). The effect of different crop stages on mean litter size was not significant. The litter size increased with the increase in the proportion of monocotyledonous grains in the diet ($R^2=0.150$, $F_{1,55}=10.13$, $P=0.002$), whereas the presence of monocotyledonous plant parts had no effect on litter size.

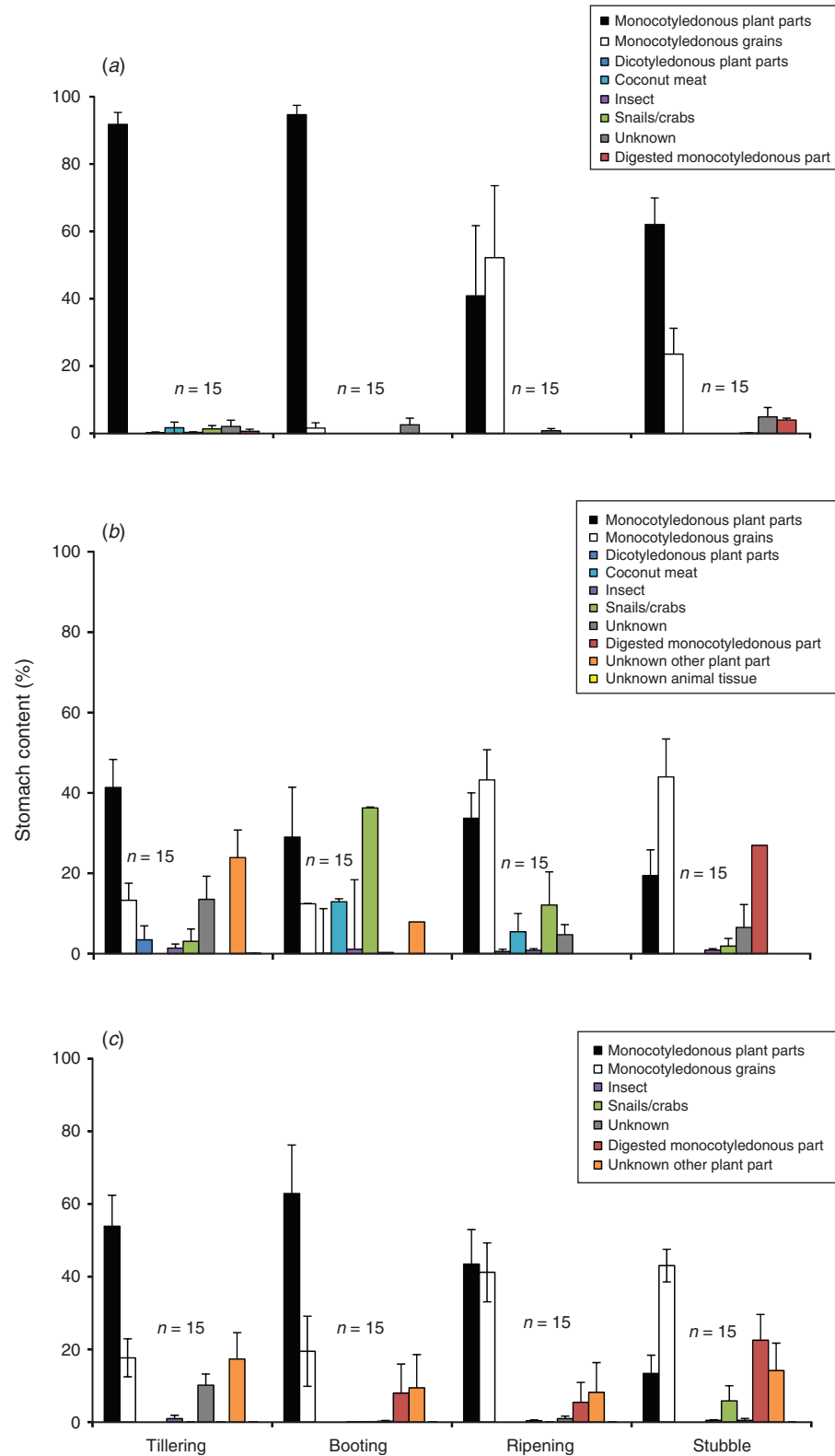


Fig. 1. Stomach content (% of diet components, mean \pm s.e.) of female (a) *Rattus tanezumi* (Laguna), (b) *R. tanezumi* (San Jose) and (c) *R. argentiventer* (San Jose) at different crop stages in a lowland rice landscape.

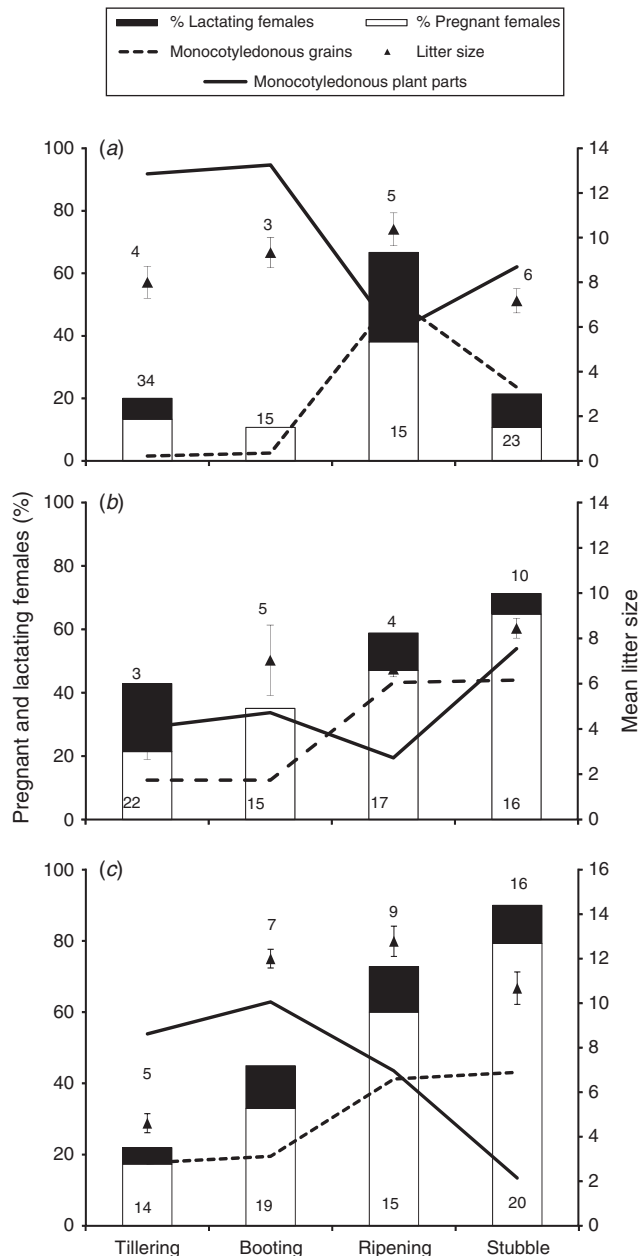


Fig. 2. Stomach content (% of diet components), breeding females (%) and litter size of female (a) *Rattus tanezumi* (Laguna), (b) *R. tanezumi* (San Jose) and (c) *R. argentiventer* (San Jose) at different crop stages in a lowland rice landscape in 2009 and 2010. Values are means \pm s.e. (i) Total number of trapped adult females is shown at the bottom of the bar graph; (ii) total number of pregnant females with visible embryos is shown at the top of the graph. Different crop stages in each season are shown at the bottom of the graph.

Diet composition and breeding performance of *R. argentiventer* in San Jose, Mindoro

The diet components of female *R. argentiventer* in San Jose over the monsoon season were monocotyledonous plant parts, monocotyledonous grains, unknown other plant parts, digested monocotyledonous plant parts, snails and crabs, and insects. No

coconut meat and dicotyledonous plant parts were present in the stomach contents. The main dietary component at the tillering and booting stages was monocotyledonous plant parts (54% and 63%, respectively), whereas at the ripening stage, the main dietary items were monocotyledonous plant parts and monocotyledonous grains (44% and 41%, respectively). The major component of diet at the stubble stage was monocotyledonous grains (43%; Fig. 1c). The mean occurrence of monocotyledonous plant parts in the diet of *R. argentiventer* at the stubble stage ($13 \pm 5.0\%$) was significantly lower than at the tillering ($54 \pm 8.5\%$, $P < 0.01$), booting ($63 \pm 13.4\%$, $P < 0.01$) and ripening ($43 \pm 9.5\%$, $P < 0.03$) stages. The occurrence of monocotyledonous grains in the diet was significantly different among crop stages ($F_{3,48} = 4.38$, $P = 0.008$); the mean occurrences of monocotyledonous grains in the diet at the stubble ($43 \pm 4.5\%$, $P < 0.01$) and ripening ($41 \pm 8.1\%$, $P < 0.01$) stages were higher than those at the booting ($19 \pm 8.1\%$) and tillering ($18 \pm 2.2\%$) stages.

The proportion of pregnant females to lactating females was different at different crop stages. More pregnant females were captured at all crop stages. Overall, the proportion of breeding females (both pregnant and lactating) of *R. argentiventer* was highest at the ripening and stubble stages of rice ($R^2 = 0.225$, $F_{3,109} = 11.23$, $P < 0.001$). The proportion of breeding females increased with the increase in the proportion of monocotyledonous grains and monocotyledonous plant parts in the diet ($R^2 = 0.130$, $F_{1,40} = 5.96$, $P = 0.019$, and $R^2 = 0.196$, $F_{1,46} = 11.24$, $P = 0.002$, respectively; Fig. 2c).

The mean litter size of *R. argentiventer* was 10 ± 1.22 ($n = 37$). The effect of different crop stages on the mean litter size was significant ($R^2 = 0.118$, $F_{1,46} = 2.51$, $P = 0.031$). The mean litter size at the tillering stage (4.7 ± 0.39) was significantly lower than that at the stubble (10.7 ± 0.67 , $P < 0.01$), booting (12.0 ± 0.88 , $P < 0.01$) and ripening (12.8 ± 0.21 , $P < 0.01$) stages. The litter size increased with the increase in the proportion of monocotyledonous grains and monocotyledonous plant parts in the diet ($R^2 = 0.170$, $F_{1,46} = 9.39$, $P = 0.004$, and $R^2 = 0.081$, $F_{1,52} = 4.06$, $P = 0.050$, respectively).

Background food availability

In Laguna, a mean of 400 kg ha^{-1} ($\pm 1.08 \text{ kg s.e.}$) of rice grains remained in the field 2 weeks after harvest. In San Jose, the mean amount of rice grains remaining 2 weeks after harvest was 1296 kg ha^{-1} ($\pm 0.98 \text{ kg s.e.}$). The amount of spilled grains in San Jose was significantly higher than that in Laguna ($t_{78} = 8.33$, $P < 0.001$).

Protein assay

The protein content of the rice plant at the tillering stage was 9.3% ($\pm 0.13 \text{ s.e.}$) and at the booting stage, it was 18.6% ($\pm 1.29 \text{ s.e.}$). The protein content of rice grain at the ripening stage was 7.3% ($\pm 0.06 \text{ s.e.}$), and for the rice grain remaining in the field 2 weeks after harvest, it was 3.3% ($\pm 0.69 \text{ s.e.}$). The protein content of rice plant parts at the booting stage was significantly ($P < 0.001$) higher than that at the tillering stage. The protein content of rice grains at the ripening stage was

significantly ($P < 0.001$) higher than that of spilled grains at the stubble stage.

Discussion

The seasonal diet of both rodent species indicated that higher protein content was associated with higher breeding performance. Therefore, the quality of the food supply may strongly influence the reproductive success of female *R. tanezumi* and *R. argentiventer* in lowland irrigated rice-cropping systems. The main breeding season for each species at the two sites began at the tillering stage and mean litter size was highest during the ripening stage. Our hypothesis that food quality is an important factor associated with the breeding of both species held. Breeding of *R. argentiventer* in An Giang Province, Vietnam, also was associated with the quality of rice grain at the generative stages (My Phung *et al.* 2011). Our study was a large-scale study replicated in space (two islands). However, the lack of replicates and the focus on food supply meant that we could not definitively discount factors such as maternal effects, and stress related to predator pressure (see Boonstra 2013), disease (Telfer *et al.* 2005) and population density (Ergon *et al.* 2011) on breeding dynamics of rice-field rats under tropical conditions. Each of these factors provides interesting opportunities for further study.

Interestingly, the proportion of snails and crabs in the diet of *R. tanezumi* in San Jose was highest at the booting stage. The golden apple snail is a major pest during the early growth stages of rice in the Philippines (Joshi *et al.* 2000). The snail provides a high source of protein (12.2%) (http://www.applesnail.net/content/various/eating_snails.htm, accessed on 13 March 2012). The quality of monocotyledonous grains and plant parts at the ripening stage could also have affected the breeding success of female rats; however, we tested the protein content of grains only, and not of other plant parts, at the ripening stage. Other plant compounds during these stages (tillering, booting and ripening) could also be involved in moderating breeding performance. Food containing either gibberellic acid (GB3) or 6-methoxybenzoxazolinone (6MBOA) compound in green vegetation (Reichman and Van De Graaff 1975), and sprouted seeds can stimulate early parturition, high litter size and a high proportion of breeding females for voles (Negus and Pinter 1966), multi-mammate rats (Leirs *et al.* 1994) and house mice (Bomford 1987a, 1987b). The effects of plant secondary compounds such as GB3 and 6MBOA compounds on the reproductive performance of rice-field rats in South-east Asia still need to be determined.

We did not capture *R. argentiventer* at the Laguna site, which is consistent with previous reports that this species does not occur on Luzon Island (see Aplin *et al.* 2003; Stuart *et al.* 2012). Our data indicated different dietary patterns for *R. tanezumi* when it is allopatric or sympatric with *R. argentiventer*. The major diet component of *R. tanezumi* in Laguna was monocotyledons, whereas in San Jose, golden apple snails and coconut meat were common in their diet. This could be because of interspecific competition between *R. tanezumi* and *R. argentiventer* in San Jose. Of interest is that although their breeding ecology is similar (Htwe *et al.* 2012), the breeding season of *R. tanezumi* is longer, which

suggests that the breeding response of *R. tanezumi* is more opportunistic than that of *R. argentiventer*.

The breeding season of *R. tanezumi* was extended beyond the growing season of rice in the lowland irrigated rice systems in Laguna and San Jose, and, to a lesser extent, for *R. argentiventer* in San Jose. These results differed from the findings from other studies of these species (Leung *et al.* 1999; Brown *et al.* 2003; Duque *et al.* 2008; Stuart *et al.* 2008). In the Philippines, some farmers practice ratoon cropping (promotion of crop regrowth after harvest) after the harvest of both the dry- and wet-season rice crop, although it is more common after the monsoon season. In San Jose, low rates of conception occurred in females at the stubble stage (Htwe *et al.* 2012). We suggest that the ratoon crop (growth of rice from the freshly cut tillers after the harvest of the rice crop) provided high-quality food and reasonable cover for both rodent species. Diet analyses of both species during the dry season are lacking. Such a study could provide a measure of the effect of ratoon cropping on the time of conception of female rice-field rats.

Farmers at the two sites had limited knowledge of good post-harvest technology, which contributed to the high levels of spilled grains in the rice fields 2 weeks after harvest. Climatic conditions (e.g. high winds) and varietal differences also influence the degree of shattering of rice before harvest or during harvest. The mean rice yield of the Filipino farmers at both sites was $\sim 3.4 \text{ t ha}^{-1}$, and the amount of spilled grains in the field was 0.4 and 1.2 t ha^{-1} in Laguna and San Jose, respectively. The protein content in spilled grains is low, but the amount of spilled grains was high in the fields. Although rates of conception were lower during the stubble stage, a high percentage of females were lactating. Therefore, the quantity of grains available may have helped meet the high energy demands of lactation. The availability of rice during the stubble stage is a probable explanation for an extended breeding season for female *R. tanezumi* and *R. argentiventer* in Laguna and San Jose.

Food-supplementation experiments in rice fields (Bomford 1987a) and wheat croplands (Ylönen *et al.* 2003) did not show a marked effect on the proportion of breeding female house mice. In the experiment of Bomford, food supplementation through artificial food stations did not significantly affect population abundance. The food stations could have led to aggregation of mice and density-dependent effects could have influenced the breeding performance of female mice. The amount of food taken by mice was not measured in the later study (Ylönen *et al.* 2003). There were spilled grains in both food-supplementation and control fields in their study. Similarly, My Phung *et al.* (2011) did not find a major impact on the breeding dynamics of female *R. argentiventer* in an intensive rice-cropping system (3 rice crops per season), following the provision of additional food along the borders of rice fields. In An Giang, the lag between harvest and the next-season rice crop was only 17–25 days; in this case, rodents could have had access to quality food throughout most of the year. The consistent availability of food resources could account for the lack of evidence that food quantity had an impact on the pregnancy rates of adult females, because females were breeding all the time.

We conclude that the quality of food may be an important factor for escalating breeding of female rice-field rats. The

quantity of food is associated with the maintenance of pregnancy and lactation. Our study supported the contention that the asynchronous planting is the main driver for high rodent population densities in the rice fields in South-east Asia (Huan *et al.* 2010; Sudarmaji *et al.* 2010; Htwe *et al.* 2012, 2013) because it extends the amount of time when high-quality and -quantity of food is available. An extension of planting by just 3–4 weeks would provide sufficient high-quality food for the young of that cropping season to breed within the same season, leading to a possible exponential population increase. Poor post-harvest technology, early or late harvesting because of unusual weather event, piling of harvested rice in the field for 7–15 days because of lack of labour, and using poor-quality seed that has off-variety rice (weedy rice) that has a high shattering rate before harvest, each could provide enough food to maintain a high proportion of breeding females for an extended period. We, therefore, recommend that synchronous planting and following best practices for post-harvest techniques (<http://www.knowledgebank.irri.org/rkb/index.php/> harvesting, accessed on 21 May 2013) should provide effective proactive actions to prevent the build-up of rice-field rat populations in a lowland rice landscape.

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